

Biology of the Big-headed Amazon River Turtle, *Peltocephalus dumerilianus* (Schweigger, 1812) (Testudines, Pleurodira): the basal extant Podocnemididae species

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Abstract

We review the extent and nature of scientific knowledge of the Big-headed Amazon River Turtle, *Peltocephalus dumerilianus*, covering distribution, morphology, taxonomy, diet, behaviour, reproduction, and ecology. We discuss the phylogenetic position of the species and its evolutionary relationships with the other podocnemidids, comparing morphological, karyological and molecular information. Also, we describe the importance of this species and its relationship with traditional Amazonian communities, including capture techniques, uses, beliefs and taboos. Finally, we comment on the conservation status of the species and the urgent need for additional studies. Besides discussing and reinterpreting published data, we provide new information from recent genetic studies, field activities and captive observations.

Key Words

behaviour, Cabeçudo, conservation, diet, distribution, ethno-knowledge, evolution, morphology, movements patterns, reproduction

Introduction

Peltocephalus dumerilianus (Schweigger, 1812) is an Amazonian aquatic chelonian with a distinctive large, robust head covered dorsally and laterally with shield-like plates (Figs 1, 2). It has maxillary and mandibular projections that form a hook-like structure, believed to be linked to predatory eating habits and the generally more aggressive behaviour compared to other Podocnemididae (Neill 1965). A further characteristic is that it lacks

the groove in the dorsal region between the eyes, present in *Podocnemis* species. Ventrally, one small barbule is present between the jaw and the neck (morphological comparisons with other extant species of Podocnemididae and identification keys are provided by Rueda-Almonacid et al. 2007). The evolutionary significance of these characteristics is yet to be explored.

Despite its ecological importance, including providing a source of livelihood for traditional local communities (Rebêlo and Lugli 1996; De La Ossa-Velásquez

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Figure 1. Representative *Peltocephalus dumerilianus* in a lake on the Tapajós River. Captured and photographed by E.G.

2007), much of the information about its biology is only available in natural history notes, in languages that are not easily accessible, or dissertations and theses that are often difficult to find. This makes it difficult to evaluate the current knowledge on the species. Furthermore, some aspects of the biology of *P. dumerilianus* can become an obstacle for data collection. For example, it mainly inhabits the bottom of black water bodies (Vogt 2008), making research in a natural environment particularly costly, and possibly discouraging studies on it.

Notwithstanding this, the studies available present us with interesting questions about this species. Two published studies on movement patterns of *P. dumerilianus*, from two areas in Brazil (De La Ossa-V and Vogt 2011; Castro 2013) present contrasting results, but the causes of these differences have never been discussed. Two studies on diet from different areas, essential for understanding the species ecology, also present discrepant results (Pérez-Emán and Paolillo 1997; De La Ossa-Velásquez 2007). When dealing with a widely distributed species, variations can be the result of local adaptations or reflect different study methods. It is not yet known whether local variations on different aspects of these behaviours are the result of independent evolutionary histories from possible genetic lineages or genetically structured populations. Thus, we provide preliminary results on the phylogeography of this species (Gentil et al. unpublished data), to

help build a scenario where these possible ecological divergences may have evolved. Data on the genetic diversity of this species are completely absent in the literature, but are necessary to help understand both evolutionary processes and the development of management and conservation strategies, especially in areas that contain genetically different populations.

We suggest ways to expand the knowledge of this turtle's natural history and evolution that can be useful in decision-making aimed at the conservation of this species. Thus, we organize and synthesize the information so far published on the biology and natural history of *P. dumerilianus*, we add observations recently made in field and captivity, indicate gaps in the knowledge of the species, as well as suggest future studies, demonstrating that there is still much to be done.

Taxonomic history

Peltocephalus dumerilianus was described as *Emys dumeriliana* Schweigger, 1812 by August Friedrich Schweigger (1783–1821). The name *Peltocephalus* derives from the union and Latinisation of the Greek word “pélte”, shield, and the Latin “cephalus”, head. The specific epithet *dumerilianus* honors the French zoologist André Marie Constant Duméril (1774–1860) (Bonin et al. 2006).



Figure 2. Adult *Peltocephalus dumerilianus*. Note the shields in the superior and lateral regions of the massive head. Captured and photographed by E.G.

It has undergone a several of nomenclature changes, including being placed in the genera *Podocnemis* Wagler, 1830 and *Chelys* Gray, 1831, and following a variety of misidentifications and synonymies, such as *Podocnemis dumeriliana*, *P. tracaxa*, and *Peltocephalus dumeriliana*. Some taxonomic revisions were carried out from specimens that historically were often taken abroad, mainly to European countries, for diverse scientific (and non-scientific) purposes. The first records are from the 1820s of specimens deposited in zoological collections in the United Kingdom (Boulenger 1889), Germany (Hoogmoed and Gruber 1983; Franzen and Glaw 2007), France (Bour 2006), and the Netherlands (Hoogmoed and Gruber 1983; Hoogmoed et al. 2010). The first known accession of this species in a Brazilian zoological collection took place in 1897, in the Museu Paraense Emílio Goeldi, Belém (Sanjad et al. 2012).

Based on morphological similarities with the Madagascan podocnemid *Erymnochelys madagascariensis* (Grandidier, 1867) it was even proposed that they could be phylogenetically closer to each other than compared to *Podocnemis* (see Neill 1965; França and Langer 2006). However, as early as 1835, Dumeril and Bibron had suggested that the morphological similarities do not justify this proximity (for more historical details, see Killebrew 1975). *Peltocephalus dumerilianus* was first used in 1839 by Diesing, but its name stabilised only in the 1990s, as a monotypic genus (details in Iverson 1992; Iverson and Vogt 2002; Rhodin et al. 2008; Vogt et al. 2013; see also section Evolutionary considerations).

Popular names

Within the indigenous people from Grão-Pará, Brazil (a former administrative unit including both modern Pará and Amazonas states), the species was called “Turará-acângauaçu” or “jurará-acangauaçu”, which meant Big-headed turtle possibly in some variant of Tupi (Prestes 1997; Fiori and Moraes 2011). Currently, the species is mainly known as “cabeçudo” (northwest Brazil), or “tracajá cabeçuda” or “cabeçuda” (mainly in the lower Amazon, Brazil).

Where this species occurs in the former Spanish South American colonies, it is often known as “cabezón”, but there may be local differences: in Colombia – “tortuga del charco” (Amazonas – Colombia), “cabezudo” (Putumayo), “cabezona” (Caquetá) (Medem 1960); in Peru – “guacamayo charapa” (Soini 1999); in French Guyana – “Peltocephale (or Podocnémide) de Duméril”. The English common name is Big-headed Amazon River Turtle. For other denominations, including indigenous ones, see Rueda-Almonacid et al. (2007), Barrio-Amorós and Narbaiza (2008), Vogt (2008) and Fiori and Moraes (2011).

Geographic distribution and occurrence

Its distribution is relatively extensive, encompassing north-eastern Ecuador, north-eastern Peru, north-east-

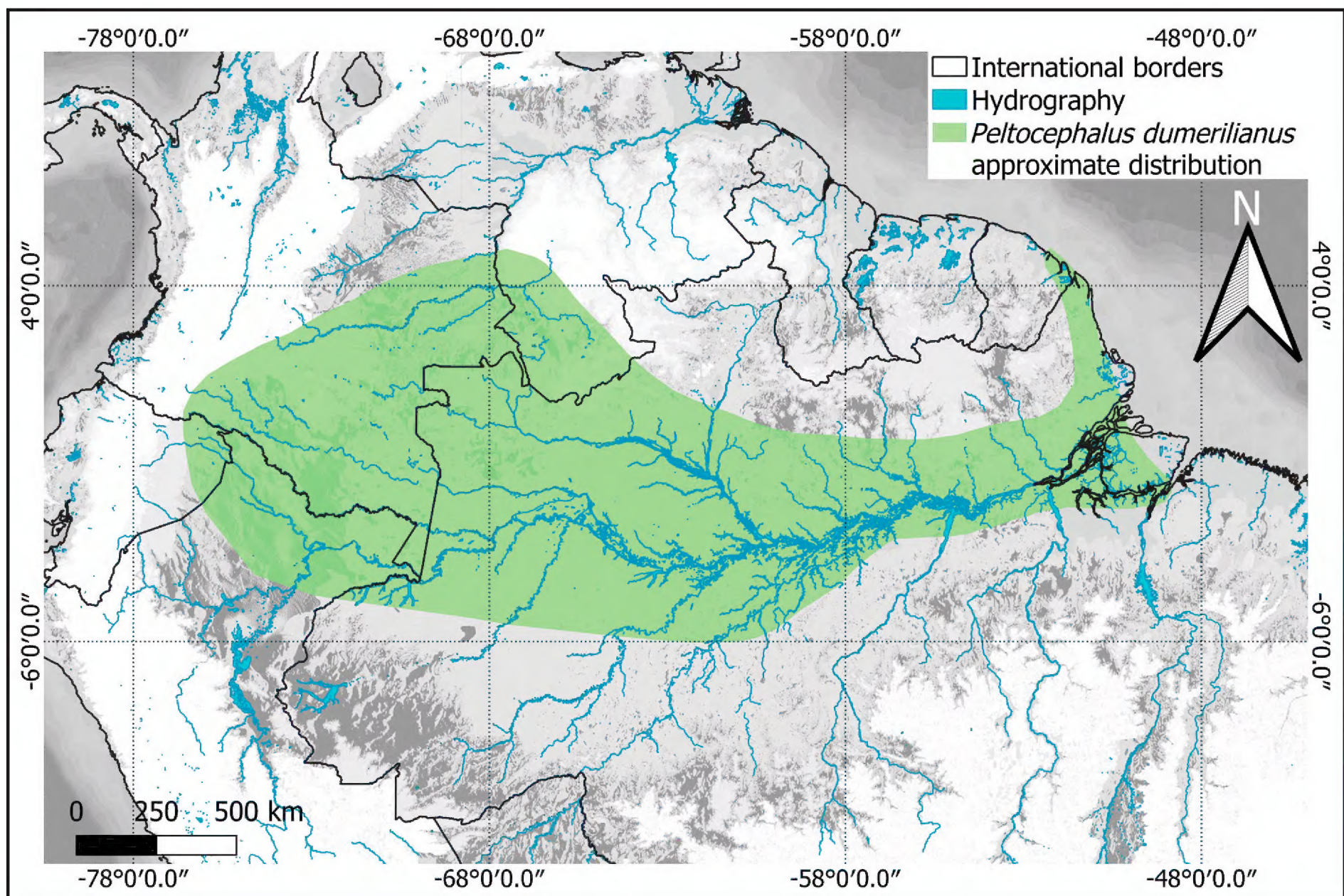


Figure 3. Approximate distribution of *Peltocephalus dumerilianus*. The area highlighted in green is based on occurrences confirmed in the literature. The distribution range includes Brazil, Colombia, Ecuador, French Guyana, Peru and Venezuela.

ern French Guyana, but occurs mainly in north-western Brazil, eastern Colombia and south-western Venezuela (Fig. 3). The occurrence in Guyana and Suriname remains controversial (Gray 1831; Iverson and Vogt 2002).

In Brazil, it occurs in greatest densities in the Negro River basin (black water environments), but is also found less frequently in regions with white and clear waters (Pritchard and Trebbau 1984; Iverson and Vogt 2002; Vogt 2008; Nascimento et al. 2012). In Colombia (Ceballos-Fonseca 2000), the Atabapo and Inírida rivers are believed to be possible historic refuges for *P. dumerilianus* (Ardila-Robayo and Barreto 2019); it is known from the Guainía (Upper Rio Negro), Isana, lower Caquetá, Vichada and Putumayo rivers (Medem 1968; see also Medem 1960). In Venezuela, it occurs in the Yagua, Atacavi (Pérez-Emán and Paolillo 1997), Autana and Sipapo rivers (Barrio-Amorós and Narbaiza 2008). In Ecuador it occurs in the Province of Pastaza, and possibly in the Province of Sucumbíos (Cisneros-Heredia 2006). In French Guyana it is uncommon and restricted to the far east of the country (Fretey 1987; Bonin et al. 2006; Böhm 2010). In Peru, it is found only in the Department of Loreto (Ferronato and Morales 2012) (Fig. 3).

Habitat

It inhabits a broad range of habitats, from white- and clear- waters, but is most abundant in black-water envi-

ronments (Wallace 1889; Vogt 2008). Commonly found in igapós (black-water Amazonian seasonally-flooded riverside forests), lakes, forest creeks (igarapés), as well as on muddy substrates (Fretey 1987; Pérez-Emán and Paolillo 1997; Rueda-Almonacid et al. 2007; Vogt 2008; Leite 2010; Parra-Henao et al. 2019). Generally occurs on the bottom of water bodies, often sheltering in cavities or under submerged tree trunks (Medem 1960; Neill 1965). In French Guyana it is found in rivers with both clear and muddy waters, as well as in swampy regions, lakes with vegetation, and in forest streams (Fretey 1987; Böhm 2010). In Colombia it can also be found in regions with shallow and fast whitewater (Parra-Henao et al. 2019).

Morphological characteristics

Sexual dimorphism

Males get larger than females (Pritchard and Trebbau 1984; Vogt 2008). The largest male had 50 cm straight length carapace and weight 15 kg, while a female was 47 cm in carapace length (Iverson and Vogt 2002). However, body size varies widely among individuals in the wild (Tables 1, 2; Medem 1983; Pritchard and Trebbau 1984; Iverson and Vogt 2002; Pezzuti 2003; Bonin et al. 2006; De La Ossa-V and Vogt 2011; Castro 2013; Parra-Henao et al. 2019). Such size variation may be linked

Table 1. Morphometric data (in cm and kg) for adult *Peltocephalus dumerilianus*. CL = straight carapace length; CW = carapace width; PL = plastron length, and PW = plastron width.

Morphometric data	French Guyana [†]	Yagua or Atacavi Rivers, Venezuela [‡]	PARNA do Jaú – AM, Brazil ^{§*}	Itú River, Barcelos – AM, Brazil	Cumicurí River, Barcelos – AM, Brazil	Trombetas River – PA, Brazil [¶]	Bojonawi Nature Reserve, Colombia [#]
CL	29.2–32.9	14–44	~16~44 (mean = 35.6)	16.5–43.4	14–45.2	38–49.9	?–46.8 (mean = 41.5)
CW	?	?	?	12.7–33.1	11.1–32.7	?	?
PL	?	?	?	13.3–34.6	12.1–35	?	?
PW	?	?	?	?	?	?	?
Mass (kg)	?	?	0.6–15.3	0.9–11.1	0.3–13.2	7–14	?–12.9 (mean = 9.9)

[†] – Fretey 1987; [‡] – Pérez-Emán and Paolillo 1997; [§] – Pezutti 2003 (*approximate values for maximum length. For other inferences, see Pezutti 2003); ^{||} – De La Ossa-Velásquez 2007; [¶] – Castro 2013; [#] – Parra-Henao et al. 2019 (For the values “?”, see fig. 3 in Parra-Henao et al. 2019).

Table 2. Morphometric data (in cm and g) for *Peltocephalus dumerilianus* hatchlings. CL = straight carapace length; CW = carapace width; PL = plastron length, and PW = plastron width.

Morphometric data	Upper Tomo River, Colombia [†]	PARNA do Jaú – AM, Brazil [‡]	Itu River, Barcelos – AM, Brazil ^{§*}
CL	4.7–5.3	5.1–6.0	4.1–5.4
CW	4.0–4.6	4.4–5.0	3.2–4.5
PL	4.2–5.0	4.3–5.2	3.8–4.6
PW	?	?	2.0–3.4
Mass (g)	25–33	25.6–37.1	26.4–34.8

[†] – Medem 1983; [‡] – Félix-Silva 2004; [§] – De La Ossa-Velásquez 2007 (*oviposition was induced and the clutch was incubated in the laboratory).

to several factors, including food availability and the size-selective impacts of anthropic pressure, needing to be further investigated (Medem 1983; Pezzuti 2003; De La Ossa-Velásquez 2007; Castro 2013).

The head of adult males is wider (the maximum width registered of an adult male being 10.5 cm; Iverson and Vogt 2002). The anterior extremity of the skull (maxillary, prefrontal, and nasal bones) is longer in adult males than in females (Iverson and Vogt 2002). Like other Podocnemididae, the tails of males are thicker and longer than those of females (Fig. 4) (Vogt 2008). Adult males have a broader and more ellipsoid slit between the anal shields (sometimes rounded in a U-shape; see Fig. 4), which in females has a more pronounced opening angle and may be V-shaped and

smaller (Iverson and Vogt 2002; see diagram in Parra-Henao et al. 2019).

Colour

Varies between individuals, age categories, and occurrence areas (Neill 1965; Fretey 1987; Iverson and Vogt 2002; Vogt 2008). Adults have a dark carapace (dark brown to black) and a lighter plastron (olive green tending to yellow). The neck and legs, proximal to the carapace, are grey to whitish (Iverson and Vogt 2002; Vogt 2008). Hatchlings have a brown carapace, with clearly-visible black sutures, which may be bordered with small orange/reddish spots. The lower edges of the carapace are yellowish, with the distal edge of the marginal shields being black. Early in their development, juveniles may have a greyish coloration with a subtle bluish luster on the head, and carapace (Gentil et al. unpublished data).

Shell

Adult individuals from Venezuela and Colombia vary noticeably from those from Brazil and French Guyana. The latter, for example, have a greater curvature of the lateral shields (Pritchard and Trebbau 1984). Carapace is

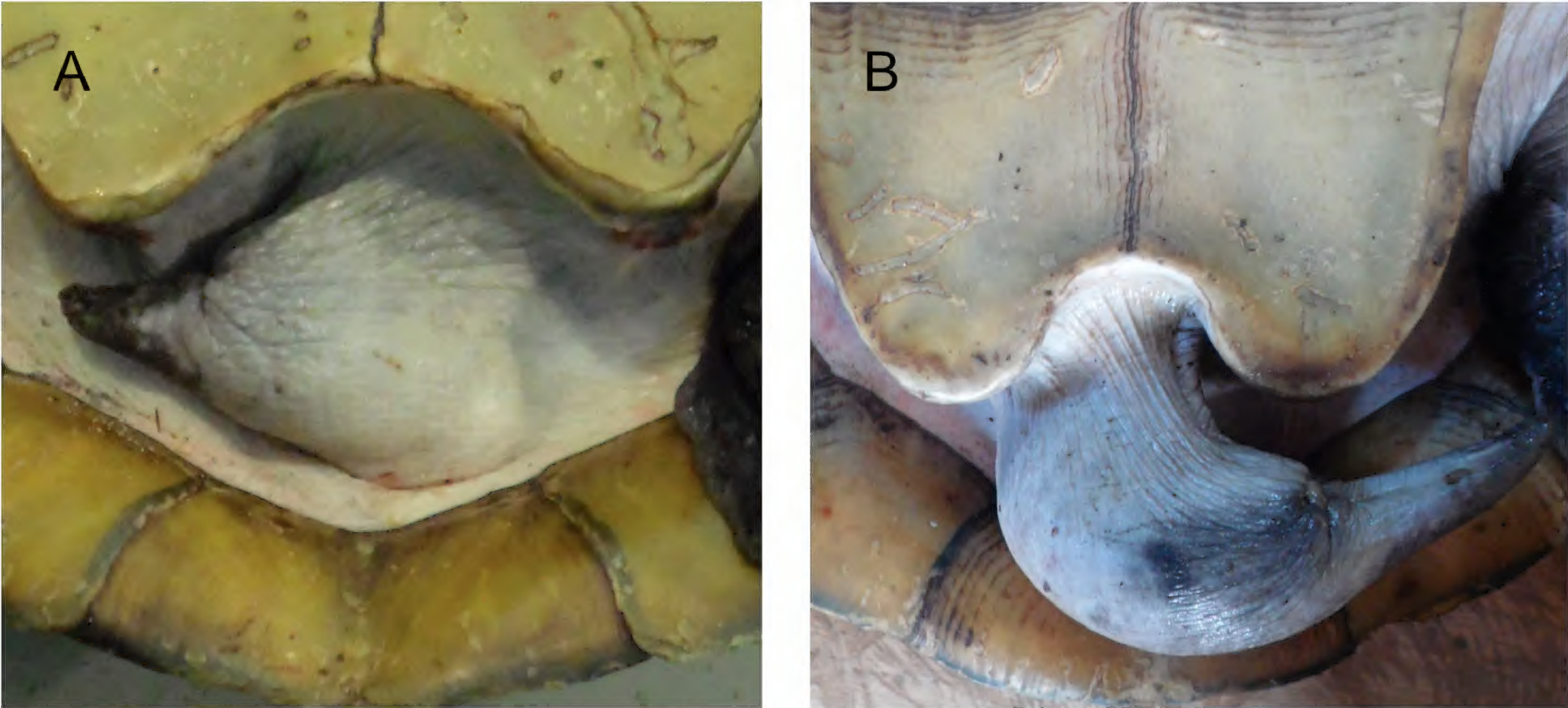


Figure 4. Tail and anal shields of *Peltocephalus dumerilianus* female (A.) and male (B.) adults.

markedly more domed compared to *Podocnemis* species (Bonin et al. 2006; Vogt 2008), and the hatchlings have a subtle keel on the carapace that is lost as the individuals age (Rueda-Almonacid et al. 2007).

Diet

Based mainly on the morphology of its head, for many years it was considered an active bottom-dwelling predator (Neill 1965); other morphological characteristics suggest otherwise. In theory, this species is not agile enough to chase prey due to the sharp curvature of its shell and the small interdigital membranes, making *P. dumerilianus* not a very efficient swimmer (Vogt 2008). Also, eating behaviours based on rapid strike are not known. Likely, it is an opportunistic predator of prey such as mollusks, small (slow) fish and aquatic or drowning insects. However, juveniles pursuit small fish in captivity (Pérez-Emán and Paolillo 1997). Carcasses in natural environments may be a frequent source of food (Table 3) (Pérez-Emán and Paolillo 1997; De La Ossa-V et al. 2011), and apparently healthy adults have been observed both in natural clear water environments and in captivity, totally immobile at the bottom of the water column with their mouths open, perhaps engaged in “sit-and-wait” behaviour (Gentil et al. unpublished data).

The current consensus is that *P. dumerilianus* is omnivorous, with a diet that may contain high proportion of both aquatic and terrestrial plant material (particularly leaves that fall into the water). Micro and macroscopic descriptions of the digestive system have really indicated omnivorous habits. The stomach main function is digestion, rather than food storage, unlike in *P. erythrocephala*, *P. expansa*, and *P. unifilis* (see Magalhães 2010; Magalhães et al. 2014 for details and comparisons with other Brazilian podocnemidids). During annual floods, the proportion of plant matter in the diet increased considerably, due to difficulty in obtaining animal-based foods (Pérez-Emán and Paolillo 1997; De La Ossa-Velásquez 2007; De La Ossa-V et al. 2011) (Table 3). However, it remains the South American podocnemidid that feeds the most on material of animal origin (Peréz-Emán and Paolillo 1997; Santos Júnior 2009; Cunha 2013; Fachín-Terán and Vogt 2014). In captivity, even 11 days-old hatchlings feed on fish when offered (Medem 1983).

The volume of animal matter found in the stomach contents averaged 51.7% in Venezuela (Pérez-Emán and Paolillo 1997), but 5.24% in Brazil (De La Ossa-Velásquez 2007). Interestingly, DNA sampling close to where these studies were carried out, verified the existence of two genetically different populations (Gentil et al. unpublished data). However, we still do not know whether these differences in diet are exclusively a consequence of the local availability of resources, considering the river flow and floods seasons, or are the result of local adaptations based on independent evolutionary histories. Its diet, overall, may have a high percentage of leaves, fruits and seeds, suggesting the species may be an important disperser, as undigested seeds have

Table 3. Taxa recorded as being ingested by *Peltocephalus dumerilianus*, from most to least frequent and listed at the lowest possible taxonomic level.

Venezuela [†]		Brazil [‡]	
Plant material	Animal material	Plant material	Animal material
<i>Thurnia polycephala</i> ^a	Fish	<i>Macrolobium acaciifolium</i> ^g	Fish
<i>Mauritia flexuosa</i> ^b	<i>Hoplosternum orinoco</i> ^g	<i>Bactris</i> sp. ^b	<i>Serrasalmus</i> sp. ^k
<i>Montrichardia arborescens</i> ^c	<i>Cichla</i> sp. ^h	<i>Astrocaryum jauari</i> ^b	Myleinae
<i>Leopoldinia pulchra</i> ^b	<i>Hoplias</i> sp. ^l	<i>Parkia</i> sp. ^g	Cichlidae
<i>Spirogyra</i> sp. ^d	<i>Goeldiella eques</i> ^l	<i>Bactris riparia</i> ^b	<i>Phractocephalus hemioliopterus</i> ⁿ
<i>Xyris</i> sp. ^e	<i>Serrasalmus</i> sp. ^k	<i>Simaba multiflora</i> ^s	Invertebrates
<i>Mauritiella aculeata</i> ^b	Invertebrates	<i>Euterpe precatoria</i> ^b	Formicidae
<i>Leopoldinia piassaba</i> ^b	<i>Pomacea</i> sp. ^l	<i>Eschweilera</i> sp. ^l	Vespidae
<i>Pradosia schomburgkiana</i> ^f	<i>Macrobrachium cortezi</i> ^m	<i>Ficus</i> sp. ^u	Blattodea
<i>Campsiandra comosa</i> ^g	Oligochaeta	<i>Calathea</i> sp. ^v	Diptera
<i>Ecclinusa</i> aff. <i>orinocensis</i> ^f	Diptera	<i>Gnetum</i> sp. ^w	Isoptera
<i>Eperua purpurea</i> ^g	Araneae	<i>Dialium</i> sp. ^g	Scarabaeinae
<i>Hevea benthamiana</i> ^b	Reptiles	<i>Pouteria</i> sp. ^f	Lepidoptera
<i>Macrolobium angustifolium</i> ^g	Pleurodira	<i>Pariana</i> sp. ^x	Araneae
<i>Macrolobium multijugum</i> ^g		<i>Cayaponia</i> sp. ^y	Ampullariidae
<i>Macrolobium</i> sp. ^g		<i>Palicourea</i> sp. ⁿ	<i>Moreirocarcinus laevifrons</i> ^o
<i>Maripa paniculata</i> ^l		<i>Abarema</i> sp. ^g	Reptiles
<i>Ouratea thyrsoidea</i> ^l		<i>Astrocaryum acaule</i> ^b	<i>Crocodilurus amazonicus</i> ^p
<i>Parinari campestris</i> ^k		<i>Macrolobium pendulum</i> ^g	Chelonia
<i>Rauvolfia polyphylla</i> ^l		<i>Dracontium</i> sp. ^c	Colubridae
<i>Spatanthus bicolor</i> ^m		<i>Alchornea</i> sp. ^h	Mammals
<i>Stachyarrhena reticulata</i> ⁿ		<i>Inga</i> sp. ^g	<i>Agouti paca</i> ^q
<i>Philodendron goeldii</i> ^c		<i>Mauritia aculeata</i> ^b	Muridae
<i>Tonina fluviatilis</i> ^o		<i>Entada</i> sp. ^g	
<i>Eleocharis</i> sp. ^p		<i>Astrocaryum</i> sp. ^b	
<i>Annona glabra</i> ^a		<i>Epiphyllum</i> sp. ^z	
Unidentified 1 ^g		<i>Ocotea</i> sp. ^f	
Unidentified 2 ^h		<i>Parkia pendula</i> ^g	
		<i>Mauritia flexuosa</i> ^b	
		<i>Couepia</i> sp. ^k	
		<i>Dichorisandra</i> sp. ^a	
		<i>Licania</i> sp. ^k	
		<i>Nectandra amazonum</i> ⁱ	
		<i>Philodendron</i> sp. ^c	
		<i>Pouteria anomala</i> ^f	
		<i>Socratea exorrhiza</i> ^b	
		<i>Theobroma</i> sp. ^B	
		<i>Buchenavia guianensis</i> ^c	
		<i>Calliandra</i> sp. ^g	
		<i>Eugenia</i> sp. ^D	
		<i>Iriartella setigera</i> ^b	
		<i>Nectandra</i> sp. ^f	
		<i>Ocotea cymbarum</i> ^f	
		<i>Zygia</i> sp. ^g	
		<i>Rollinia exsucca</i> ^a	
		<i>Costus</i> sp. ^E	
		<i>Duguetia</i> sp. ^q	
		<i>Ludwigia</i> sp. ^F	
		<i>Rollinia</i> sp. ^q	

Obs. 1 – Seeds found entire in the large intestine: *Euterpe precatoria*, *Mauritia flexuosa*, *Astrocaryum jauari*, *Dracontium* sp., *Socratea exorrhiza*, *Macrolobium acaciifolium*, *Ficus* sp. Obs. 2 – Letters after each item indicate the Family, when taxonomic identification at a lower level was possible: ^aThurniaceae; ^bArecaceae; ^cAraceae; ^dZygnemataceae; ^eXyridaceae; ^fSapotaceae; ^gFabaceae; ^hEuphorbiaceae; ⁱConvolvulaceae; ^jOchnaceae; ^kChrysobalanaceae; ^lApocynaceae; ^mRapateaceae; ⁿRubiaceae; ^oEriocaulaceae; ^pCyperaceae; ^qAnnonaceae; ^rLauraceae; ^sSimaroubaceae; ^tLecythidaceae; ^uMoraceae; ^vMarantaceae; ^wGnetaceae; ^xPoaceae; ^yCucurbitaceae; ^zCactaceae; ^ACommelinaceae; ^BMalvaceae; ^CCombretaceae; ^DMyrtaceae; ^ECostaceae; ^FOnagraceae; ^GCallichthyidae; ^HCichlidae; ^IErythrinidae; ^JHeptapteridae; ^KSerrasalmidae; ^LAmpullariidae; ^MPalaemonidae; ^NPimelodidae; ^OTrichodactylidae; ^PTeiidae; ^QCuniculidae. [†] – Pérez-Emán and Paolillo 1997; [‡] – De La Ossa-Velásquez 2007.

been observed in its intestines (for extra information on diet composition, see Pérez-Emán and Paolillo 1997; De La Ossa-Velásquez 2007; De La Ossa-V et al. 2011) (Table 3).

Diet can also be inferred based on metals accumulation in specimens captured in Amazonas, Brazil. The concentration of mercury (Hg) in the muscles had a mean value of 106 ppb, the highest for the surveyed Podocnemididae (Schneider 2007). This indicates a more generalist diet, with a higher proportion of material of animal origin, compared to the other species studied (Schneider 2007; Schneider et al. 2010). For comparison, in the purely carnivorous *Chelus fimbriata* (Schneider, 1783), mean Hg concentration was 433 ppb, while in the largely herbivorous *Podocnemis erythrocephala* it was 33 ppb (Schneider 2007; Schneider et al. 2010). Selenium (Se) levels obtained in blood samples of studies species ranged from 538 ppb (*P. dumerilianus*), 463 ppb (*C. fimbriata*), 276 ppb (*Podocnemis sextuberculata*) and 164 ppb (*P. erythrocephala*) (Burger et al. 2009, also providing details on arsenic, cadmium, chromium, lead, and Hg). The greatest amount of Se found in *P. dumerilianus* is, perhaps, due both to the ingestion of fish, aquatic invertebrates and carrion, as well as the greater proportions of fruits and seeds ingested by this species, the latter being recognised as the largest sources of selenium in adult plants (Terry et al. 2000; Pilon-Smits 2019). The difference in Se values found between *C. fimbriata* and *P. dumerilianus* was not significant (Burger et al. 2009). Perhaps this can be explained because *C. fimbriata* is a carnivorous species that feeds mainly on aquatic invertebrates and fish, rich in Se (Mason et al. 2000). The analysed *Podocnemis* species usually eat non-seed plant parts poor in Se (Souza 2005; Vogt 2008; Fachín-Terán et al. 2014), likely producing the differences to the concentrations observed in *P. dumerilianus* (Burger et al. 2009).

Tissue ^{13}C stable isotope concentrations ($-30.48 \pm 0.27\text{‰}$ in *P. dumerilianus* and $-31.59 \pm 0.76\text{‰}$ in *P. erythrocephala*) suggested that the main source of energy for *P. dumerilianus* is igapó forest plant species, while for *P. erythrocephala* it was a mixture of forest-derived material (such as fruits and seeds), combined with periphytonic algae (see Souza 2005).

Peltocephalus dumerilianus appears to have diet with high plasticity. Captive individuals in French Guyana survived well on a carnivorous diet, even consuming red meat (Fretey 1987), while captive juveniles in Colombia fed on small live fish, water snails and earthworms, and vegetables (Medem 1983; for general comparisons with other South American Podocnemididae species, see Eismberg et al. 2016; for details on food items eaten, see Pérez-Emán and Paolillo 1997; De La Ossa-Velásquez 2007). Opportunistic cannibalism has been recorded in nature, with the ingestion of con-specific eggs by a female (De La Ossa-V et al. 2009a).

General behaviour

In Colombia and Brazil, *P. dumerilianus* is more active at dusk and at night, increasing sampling efficiency at these

times (Parra-Henao et al. 2019; Gentil et al. unpublished data). Also in Colombia, not all captive hatchlings exposed themselves to the sun, and moved less and spent more time hidden under the leaves inside the aquarium, unlike individuals of *Podocnemis expansa*, *P. unifilis* and *P. vogli* (Medem 1983). Perhaps this explains why it is so difficult to find juveniles in situ. However, this behaviour should be further investigated as temperature is known to influence hatchling feeding activity in captivity (De La Ossa-V et al. 2009b), as well as affecting adult movement patterns in the wild (Castro 2013).

The distinctive shape and size of its head is, perhaps, more associated with defence than predation, especially considering its combative nature. Aggressive behaviour was well known and reported by the indigenous peoples of Brazil (Prestes 1997; Fiori and Moraes 2011). A child had its knee seriously damaged (Vogt 2008), and riverside rural communities (known as “ribeirinhos”) often report cases of adults who have had fingers mutilated by bites from this turtle. In addition, out of water, this turtle can deliver very powerful blows with their legs and sharp claws, which can also cause painful injuries. Even juvenile individuals have a powerful bite, strong enough to dismember and even tear off pieces of con-specific’s plastron (De La Ossa-Velásquez 2007). Captive juveniles tear flesh easily with the help of their front claws; they can also scrape the flesh off bones, using their mouthpieces that work like scissors (Gentil et al. unpublished data).

Despite this aggressiveness, adults in the wild and juveniles in captivity seem not to be territorial (De La Ossa-V et al. 2009b; De La Ossa-V and Vogt 2011). However, captive *P. dumerilianus* can also be highly aggressive towards other turtle species, biting them and sometimes even killing them (De La Ossa-Velásquez 2007; Andrade 2008; Barrio-Amorós and Narbaiza 2008).

Reproduction

Peltocephalus dumerilianus is the only extant species of South American Podocnemididae that, so far, has not been found nesting on sandy beaches (Vogt 2008; Páez et al. 2012). Instead, they lay eggs in solitary and concealed nests in a wide range of locations, making nests difficult to find and decreasing egg-loss to predators (Vogt 2008). Laying in sandy soils does occur, but is very rare, and only when leaf-litter is present (Medem 1983; Félix-Silva 2004). Females lay close to banks of forest streams, in igapó areas under the influence of flooding, under foliage in clearings or beneath vegetation (shrubs, grasses), within termite mounds, in sandy ravines close to water bodies, in between the roots of fallen logs, and even in recently-burned areas (Medem 1983; Vogt et al. 1994; Rebêlo and Lugli 1996; Pezzuti 2003; Félix-Silva 2004; Vogt 2008). However, it is possible that females are selective, and that all such places share yet undetermined common features which make them suitable as nesting sites (Medem 1983).

Most nests (56.3%; N = 18) in a targeted study were recorded in areas impacted by burning (Félix-Silva 2004). Nonetheless, it is unlikely that these areas are used preferentially for egg laying, since (i) such fires would have been infrequent during most of the evolution of the species, and (ii), perhaps the main reason, because of the toxins present in the soil following fires. Such toxins/pollutants (carbon monoxide, as well as sulphur and nitrogen derivatives, for example), including soot itself, could kill embryos through the gas-permeable eggshell by suffocation and intoxication. In fact, eggs in burnt areas had a lower hatching rate than the nests laid in unburnt igapós (Félix-Silva 2004). Possibly the females have some memory-based level of loyalty to the places where they have oviposited in the past, a conjecture supported by the fact that individuals of this species do not migrate great distances (De La Ossa-V and Vogt 2011; Castro 2013).

Overall, the shape of the *P. dumerilianus* nest resembles a vertically inclined bottle (Medem 1983), depth and dimensions vary with the terrain in which the nest is dug, as well as the physical condition of the excavating female, among other factors (see Medem 1983; Félix-Silva 2004; Vogt 2008). A characteristic that can be used to infer the time that laying occurred is the presence of the viscous mucous film on the surface of the eggs, which disappears after around two weeks after oviposition (Medem 1983; Vogt 2008). Eggs are sometimes separated into two groups, one at each end of the nest bottom, which can give the false appearance of two independent nests (Vogt 2008). Hatchlings use an egg-tooth to hatch what can remain for up to 45 days before shedding (Medem 1983).

The laying season, and the quantity, dimensions and the incubation time of the eggs appear to vary according to the environmental characteristics of each location (Table 4) (Medem 1983; Félix-Silva 2004; De La

Ossa-Velásquez 2007). Similar to many podocnemid species, the sex of *P. dumerilianus* individuals is determined by temperature (Vogt et al. 1994; De La Ossa-Velásquez 2007), which can result in a local variation in population sex ratios (Félix-Silva 2004; De La Ossa-Velásquez 2007; for information on architecture and temperature of the nests, see Félix-Silva 2004).

The smallest captured egg-containing female had a total carapace length of 25.2 cm (De La Ossa-Velásquez 2007). Clutch size and egg shape change as the female ages and grows, with larger females producing more and larger eggs (De La Ossa-Velásquez 2007). Macroscopic analysis of ovaries and oviducts suggests that egg-laying occurs only once a year, and that oviposition is related to the local hydrological cycle, a pattern common in the Podocnemididae (De La Ossa-Velásquez and Vogt 2011). Nonetheless, possibly egg-laying may occur twice annually (R.C.V. unpublished data).

Movement patterns

Peltocephalus dumerilianus is generally considered to be a less agile swimmer than other podocnemids, incapable of long-distance aquatic dispersal (Neill 1965; Vogt 2008). This is based on morphological characteristics such as the carapace curvature being visibly more accentuated than in similarly-sized species of *Podocnemis*, which would hinder the hydrodynamics, and the interdigital membranes being less well-developed than other Podocnemididae, providing weaker propulsion (Vogt 2008).

Radio transmitters have been used to study *P. dumerilianus* movements' patterns, at two locations 1,100 km apart in Brazil (De La Ossa-V and Vogt 2011; Castro 2013). A 12-month study on the Rio Negro, at Barcelos, Amazonas state, found that females covered greater distances (7.42 km) than males (5.72 km), but there were no significant differences in home range area by sex or size (mean $\approx$ 9 km²). However, there was an overlap of the home ranges in relation to the sexes (De La Ossa-V and Vogt 2011). On the Trombetas River, Pará state, both water temperature and the different phases of the local hydrological cycle influenced movement patterns; during the flooding season, individuals moved less, with greatest movement rates during both low water and when water temperatures were lower (Castro 2013). As with the individuals studied at Barcelos, there were no differences in home ranges between sexes or size (Castro 2013; mean = 4.27 km²). However, there were no marked differences in distances travelled, as females moved 10.54 km and males 12.38 km (Castro 2013). Possibly, the differences in these results are more a reflection of methodological, rather than biological differences. Individuals may have restricted lifetime home ranges: one tagged male was recaptured after 19 years, in the same stream where he was originally marked as hatchling (Castro 2013).

Table 4. Dimensions of *Peltocephalus dumerilianus* eggs laid in different locations.

Locality	Oviposition season	Number of eggs	Dimensions (cm) width – length	Mass (g)	Incubation duration
Colômbia – Upper Tomo River†	December	8–16	5.0–6.2 3.3–4.3	36.5–51	Approx. 100 days*
Venezuela‡	Between December and April	7–25	?	?	?
Brazil – Trombetas§	August and September	3–25	5.0–5.8 3.4–3.9	39–50	Approx. 124 days
Brazil – Jaú¶	September and October	8–22	5.2–6.1 3.3–3.6	37.3–45.5	Between 106 and 135 days
Brazil – Barcelos¶	Between August and October	7–13*	4.7–6.2 3.5–4.3	36.7–48.5	96–98* days

† – Colômbia – Medem 1983 (* the eggs were removed to the laboratory) (In Medem 1960 (and Medem 1983) it is reported by natives that the laying on the Amazon River is up to 10 eggs and that they nest between July and August in this location). ‡ – Venezuela – Pérez-Emán 1990 (apud Barrio-Amorós and Narbaiza 2008) Pritchard and Trebbau 1984; § – Brazil – Trombetas – Vogt et al. 1994; ¶ – Brazil – Jaú – Félix-Silva 2004; ¶ – Brazil – Barcelos – De La Ossa-Velásquez 2007 (*laboratory incubation period).

Predators

Due to the nest characteristics, the extent of natural nest depredation and the species responsible for such losses remain poorly-known (Félix-Silva 2004; Gentil et al. 2021 in press). Based on reports from local inhabitants, the main nest-robbing species are the lizards *Tupinambis teguixin* (Linnaeus, 1758), *Crocodilurus amazonicus* (Spix, 1825), *Iguana iguana* (Linnaeus, 1758), the primate *Cebus albifrons* (Humboldt, 1812), felid *Panthera onca* (Linnaeus, 1758) and falconiform *Daptrius ater* Vieillot, 1816 (Medem 1983; Félix-Silva 2004).

Hatchlings suffered some 60.5% of mortality (N = 526 individuals) due to fly larvae (Vogt et al. 1994). Adults are preyed upon intensely by humans and are presumably eaten by alligators, pumas and jaguars that are known to feed on *Podocnemis* species (Salera Júnior et al. 2009).

Parasites

Peltocephalus dumerilianus may be infected with *Eimeria peltocephali* (Lainson and Naiff 1998a) and *Haemoproteus peltocephali* (Lainson and Naiff 1998b), protozoan blood parasites which are commonly found in mollusks, annelids, arthropods and other invertebrates (Wenrich 1935).

Due to the wide consumption of *P. dumerilianus* in Amazonia, there is the possibility of human contamination when infected and poorly-prepared animals are eaten (Aguirre et al. 2006; Magnino et al. 2009). Possibly an infection by *Salmonella* Lignieres, 1900 in humans was due to *P. dumerilianus* egg consumption (Maroja and Lowery 1956). For species that parasitize *P. dumerilianus* and other podocnemidids, as well as the impacted organs, see Sarmiento (1959), Gomes and Kohn (1970), Široký et al. (2006), Muniz-Pereira et al. (2009), Pineda-Catalan et al. (2013), Fernandes and Kohn (2014), Silva (2014), Novelli et al. (2014), and Ferreira (2016).

Evolutionary considerations and position within Podocnemididae

Molecular and cytogenetic research has contributed extensively to the understanding of the evolutionary relationships in Podocnemididae, and also helped to clarify taxonomic problems in *P. dumerilianus* (see taxonomic history and morphological characteristics sections).

In the 1970s both the Big-headed Amazon River Turtle and the Madagascan Big-headed Turtle were considered to belong to the genus *Podocnemis* (*P. dumeriliana* and *P. madagascariensis*, respectively) (see Frair et al. 1978; Hoogmoed and Gruber 1983). However, blood biochemistry studies showed that *P. dumerilianus* and *E. madagascariensis* differed extensively from the genus *Podocnemis*, indicating that neither species should be allocated

to this taxon. In addition, the two species were sufficiently different from each other that they could not be placed in the same genus (Frair et al. 1978). Consequently, the Big-headed Amazon River Turtle was placed in the monotypic *Peltocephalus*, while Madagascan Big-headed Turtle – *Erymnochelys*, following the suggestions by Dumeril and Bibron (1835) and Baur (1888) (Williams 1954) respectively, almost a century before.

The development of molecular techniques allowed precise genetic analyses that revealed the main evolutionary relationships in extant Podocnemididae with even greater clarity. While for some authors, similarities in morphological characteristics relate *Peltocephalus* and *Erymnochelys* phylogenetically, mitochondrial genes sequencing indicated that *Erymnochelys* was more closely related to *Podocnemis* (Georges et al. 1998; Noonan 2000), and similarities were possibly due to convergence.

This pattern was also confirmed with the karyotypes available for all extant species in the family: *P. dumerilianus* has $2n = 26$ chromosomes, while all other species have $2n = 28$ (Ayres et al. 1969; Rhodin et al. 1978). The Fundamental Number (FN, the number of chromosomal arms) is 52 for *P. dumerilianus* and 58 in *E. madagascariensis*, while in *Podocnemis* species FN is 52 or 54. Both *P. dumerilianus* and *E. madagascariensis* have only chromosomes with two arms, while *Podocnemis* species also have acrocentric chromosomes (with only one chromosomal arm) (Ayres et al. 1969; Rhodin et al. 1978; Bull and Legler 1980; Fantin and Monjeló 2011; Cavalcante et al. 2018). Banding with telomeric probes in an interstitial position have been found in *Podocnemis* species, which suggests that numerous chromosomal rearrangements have occurred in this genus (Noronha et al. 2016; Cavalcante et al. 2018, 2020). Tagging *P. dumerilianus* telomeric regions did not provide evidence of similar rearrangements, as chromosomes were all marked only in the final position of the arms (Ventura et al. 2014).

Nuclear and mitochondrial gene data have been used to clarify Podocnemididae phylogenetic relationships. From a dated tree, it was inferred that the origin of *P. dumerilianus* occurred in the Cretaceous (Thomson et al. 2021), approximately 86 million years ago, this being the basal species among the extant podocnemidids (Vargas-Ramírez et al. 2008). Around 78 million years ago, the divergence occurred between *Erymnochelys* and the ancestor of *Podocnemis*. Finally, diversification within the genus *Podocnemis* began during the Tertiary, approximately 37 million years ago (Vargas-Ramírez et al. 2008). Unfortunately, presently there are no known *Peltocephalus* fossils that could provide accuracy to time estimates for the origin of this species (for morphological comparisons between *P. dumerilianus* and fossil species, see Gaffney et al. 1998; De La Fuente 2003; Gaffney and Forster 2003; França and Langer 2006; Matiazzi 2007; Cadena et al. 2010; Gaffney et al. 2011; Cadena et al. 2012; Dumont Júnior 2013; Cadena 2015; Carvalho 2015; Ferreira et al. 2015; Cadena et al. 2020).

Molecular data, apparently, tell a similar evolutionary story to cytogenetic data. However, given such a long

evolutionary history, including a continental drift, many processes of diversification within *P. dumerilianus* doubtless await discovery. A preliminary phylogeographic study of *P. dumerilianus*, based on mitochondrial genes, points to the existence of three genetically differentiated populations with occurrences partially related to the Orinoco and Amazon basins, whose divergence began in the Pleistocene (Gentil et al. unpublished data). During this period major changes occurred in the respective basins, and are associated with divergence events in other aquatic species such as fish, river dolphins, and otters (Willis et al. 2010; Hollatz et al. 2011; Wesselingh and Hoorn 2011; Ruiz-García et al. 2018).

Beliefs and use of the Big-headed Amazon River Turtle in traditional communities

Within Amazonia, *P. dumerilianus* is used as food, for medicinal purposes, and ornamentation for home and personal use (Alves et al. 2012), and the blood is used as a potent ant killer (Silva 2008). In Pará (Brazil), the species is used as food, and serves medicinal (anti-inflammatory, treatment for snake bites and even for strokes) and cosmetic (fat is used for the skin and the hair) purposes. Paradoxically, it was also one of the species most commonly cited as being taboo (Félix-Silva et al. 2018).

For example, some ribeirinho families believe that pregnant women cannot consume *P. dumerilianus* meat because it is “reimosa” (possessed of a strong and disruptive power), and so can harm the health of such a person (Piperata 2008). Even in Jaú National Park, where it is widely consumed by the locals, some believe that the meat of “cabeçudo” is bad for the stomach (Rebêlo and Pezzuti 2000). These cases can perhaps be explained by extrapolation from some events in which specific people suffered digestive problems after consuming this animal. Furthermore, ribeirinhos believe that the consumption of male specimens can cause inflammations, and that eggs can only be eaten cooked, otherwise they can cause tumors (Pezzuti 2003).

Although some parts of *P. dumerilianus* have a protein content similar to widely accepted bush meat species such as peccary (*Pecari tajacu* (Linnaeus, 1758)), paca (*Cuniculus paca* (Linnaeus, 1766)), and agouti (*Dasyprocta fuliginosa* Wagler, 1832) (Aguiar, 1996), there is strong regional variation in the use of the species as food. In some areas of occurrence, those consuming Big-headed Amazon River Turtles are frowned upon by the community, as the species is associated with the poorest and/or a lack of ability/luck to capture “nobler” animals. What gave rise to this belief pattern is unknown. However, it has been known in general society since at least the 18th century, when consumption of this chelonian was already associated with the poorest indigenous and ribeirinho peoples (Fiori and Moraes 2011).

Capture techniques

Peltocephalus dumerilianus is generally either captured manually or with the help of a jaticá (a special turtle-hunting arrow: Pezzuti 2003; De La Ossa-Velásquez 2007). However, it can also be captured with the aid of hooks (Smith 1979), as well as trammel and fyke nets (Vogt 1980).

Alfred Russel Wallace witnessed and described in detail a highly efficient indigenous method for capturing turtles. To avoid arrows ricocheting off the turtle carapace, as would occur if fired directly, the Indians fired the arrow upwards so that it would fall vertically on to the turtle’s shell. The arrowhead was not fixed, but only supported on the tip of the shaft, to which it was further attached by a string. With the impact of the arrow into its shell the turtle dived, but the rod floated and in this way the now-tagged and located chelonian could then be captured. The technique was so refined that most turtles sold in markets had the marks of arrows on their shells (Wallace 1889).

Perhaps the modern jaticá is a simplified adaptation of the technique described by Wallace. The jaticá, like the indigenous arrow described above, has a point (usually made of steel, and some 5–8 mm in length) that is only supported on the tip of a wooden shaft and attached by a string. The rural fishermen also deploy a wooden rod (called a “baliza” or beacon) onto one end of which a piece of fish or meat (usually rotten) is impaled. This end is then driven into the substrate, under water. The ribeirinho remain in their canoe and watch for movements of the baliza caused by attacking carnivores. Depending on how the baliza moves, the ribeirinho can tell if the visitor is a Big-headed Amazon River Turtle (or sometimes another chelonian) and not piranha fish, for example. The next step is to strike the chelonian shell vertically with the jaticá. If the steel tip attaches to the shell then the animal is hauled into canoe or in to the riverside (technique taught to E.G. by an experienced ribeirinhos).

Conservation status and threats

Peltocephalus dumerilianus is listed in CITES Appendix II and was considered Vulnerable – A1acd by the IUCN, but the assessment was made in 1996 (TFTSG-IUCN 1996). Given the anthropogenic pressures, environmental degradation throughout its distribution range, including contamination of rivers by mining activities, pesticides, deforestation of riparian vegetation, and construction of hydroelectric enterprises (Laurance et al. 2001; Neves et al. 2018; Vasco et al. 2021), the current conservation status of this turtle can be worse. Like other South American podocnemids, *P. dumerilianus* has probably been consumed since the arrival of the first Amazonian inhabitants. Existing records date from post-Colombian times and show intense human predation on river turtles, among them *P. dumerilianus* (Wallace 1889; Fiori and Moraes 2011).

During his expedition along the Negro and Orinoco rivers, Wallace had frequent contact with *P. dumerilianus*. In fact, he and his team often fed on this species. In an indigenous village on the upper Rio Negro, following an exchange for salt with indigenous people, Wallace had access to a specimen that was sufficient to feed eight people, with some still left-over for the next day. This must have been an unusually large individual, but unfortunately no information concerning its dimensions is included in Wallace (1889). Close to the Cassiquiare Canal, on the upper Rio Negro, Wallace recorded that the inhabitants used to pen Big-headed Amazon River Turtles and fish as food-sources during periods of food scarcity. At the same time, although these turtles were still frequently captured, natives told him they were becoming rarer (Wallace 1889).

Although it is still considered abundant in the Negro River basin, *P. dumerilianus* is widely captured throughout the year and has been for many years (Wallace 1889; Rebêlo and Lugli 1996; Pezzuti 2003; De La Ossa-Velásquez 2007; Vogt 2008; da Silva and Begossi 2009; Pezzuti et al. 2010; Schneider et al. 2011). The conservation status of the species is not known in all countries where it occurs, since studies are scarce and incomplete (for more details of the status of local populations and their threats: Brazil – Vogt 2008; Colombia – Castaño-Mora 1997; Páez et al. 2012; Bock and Páez 2017; Ecuador – Cisneros-Heredia 2006; French Guyana (where, at least in recent decades, this species has been considered rare) – Fretey 1987; Böhm 2010; Peru (critically endangered) – Ferronato and Morales 2012; Venezuela – Hernández and Espín 2003; Barrio-Amorós and Narbaiza 2008). An estimated 74% of turtles captured by ribeirinhos in Jaú National Park (JNP), Brazil, between 1992 and 2000 were *P. dumerilianus* and *P. unifilis* (Rebêlo et al. 2005). In JNP, it is captured mainly for consumption as food, although about 15% are sold or exchanged (Rebêlo and Lugli 1996). In Barcelos, up to 50% of captured specimens were sold to obtain funds to buy other items necessary for ribeirinho life (De La Ossa-Velásquez 2007). The “cabeçudo” is widely (if illicitly) commercialised in rural Amazonia by a network of rural hunters, urban market-sellers and their middlemen. In 2010, specimens of *P. dumerilianus* from the Rio Negro purchased rurally for US\$2 to US\$10, could cost up to US\$100 in markets of Manaus (Pezzuti et al. 2010; Schneider et al. 2011).

In Venezuela, consumption of *P. dumerilianus* is widespread, but there is little quantitative data. One estimate was that more than 1,000 specimens of *P. dumerilianus* were extracted from nature, per year, in wildcat mining gold areas, but taking into account that in these areas there were up to 3,000 wildcat gold miners, this may be an underestimate (Barrio-Amorós and Narbaiza 2008). Between 200,000 and 400,000 specimens of *P. dumerilianus*, along with *P. erythrocephala* and *P. unifilis*, were estimated to be predated by humans in just one year (Gorzula 1995). In 1998, in the illegal gold mining areas, adult specimens were sold for up to US\$50 each (Barrio-Amorós and Narbaiza 2008). In Colombia, where river turtles are con-

sumed during religious festivals, up to 1,000 specimens of *P. dumerilianus* and *P. erythrocephala* were used in a single event (Castaño-Mora 1997). Therefore, although eggs and juveniles are difficult to find (Vogt 2008), adults are intensively preyed upon by humans (Wallace 1889; Gorzula 1995; Gorzula and Señaris 1998; Rebêlo and Pezzuti 2000; Hernández and Espín 2003; Pezzuti 2003; Fachín-Terán et al. 2004; De La Ossa-Velásquez 2007; Vogt 2008; Alves 2012; Alves et al. 2012; Waldez et al. 2013; Morales-Betancourt et al. 2015). There is an urgent need for the impacts of this use to be assessed.

Much research is still needed to effectively and accurately estimate the conservation status of *P. dumerilianus* at the full range, in national, regional and populational levels. Even morphometric data, crucial information to determine effective conservation practices, are not currently available at appropriate levels (as can be seen in Tables 1, 2, 4), and growth in the wild is based on a single observation, of a male marked as a hatchling and recaptured 19 years later, when it weighed 7 kg and had straight-line carapace length of 38 cm (Castro 2013). Furthermore, the restricted and localised habitat use combined with low inter-population and inter-regional migration means that urgent preservation of their environments is recommended (Castro 2013).

Prospects for future research

In view of the IUCN categorisation of the species as Vulnerable, the growing anthropic pressure, the lack of information about different aspects of its biology, and the marked behavioural differences between *P. dumerilianus* and other podocnemidids, it is urgent to carry out studies on the genetic structure of populations range-wide, as well as diversity within these populations aimed at a greater understanding of its evolutionary history. The best evolutionary knowledge on such an ancient species can, in addition to improving what is known about itself, provide pieces that can help assemble the puzzle of the often tricky history of Amazonian landscapes.

More basic information on morphometry in different areas, in both sexes, as well as determining the size of individuals at the onset of reproduction, is required. The determination of the short- and long-distance movements and home range are currently restricted to two locations, despite a wide distribution. In view of the discrepancy in the results, it is important to know if there is a common pattern of movement, or if this regional variation occurs in a generalised way, as well as whether laying-site fidelity occurs.

Studies of regional diet variation would provide valuable information on differences in growth and migration patterns, trophic position and reaction to environmental disturbances. For this, the combined use of such techniques as stomach-flushing and analysis of stable isotopes in different habitats, such as black, white and clear waters, would provide a robust understanding of this aspect of *P. dumerilianus* ecology.

All of this information is essential for a thorough understanding of the aspects of the ecology, behaviour, reproduction and development of *P. dumerilianus*, which can then be used to identify the most threatened populations, assist in the elaboration of conservation strategies, such as reproduction in captivity for possible reintroduction into the wild, and support decision-making for priority areas for conservation of this ancient species.

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